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# **Title: The Serengeti squeeze: cross-boundary human impacts compromise an iconic protected ecosystem**

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**Abstract:** Protected areas provide major benefits for humans in the form of ecosystem services, but landscape degradation by human activity at their edges may compromise their ecological functioning. Using multiple lines of evidence from 40 years of research in the Serengeti-Mara ecosystem, we find that such edge degradation has effectively “squeezed” wildlife into the core protected area and has altered the ecosystem’s dynamics even within this 40,000 km<sup>2</sup> ecosystem. This spatial cascade reduced resilience in the core and was mediated by the movement of grazers which reduced grass fuel and fires, weakened capacity of soils to sequester nutrients and carbon, and decreased responsiveness of primary production to rainfall. Similar effects in other protected ecosystems worldwide may require rethinking of natural resource management outside protected areas.

**One Sentence Summary:** Anthropogenic impacts at the edges of an ecosystem change the ecological functionality at the core

**Main Text:** Biodiversity is critical for sustaining ecosystem services (1–4), yet the major challenge is how to conserve it. Protected areas (PAs), in which human activities such as hunting, grazing, logging or conversion to cropland are restricted represent the dominant conservation strategy worldwide (5), despite potential conflicts of interest with historic rights or well-being of indigenous people (6). However, the sustainability of the PA strategy to preserve biodiversity and ecosystem services is uncertain. One third of PAs are under intense human pressure globally (7), especially from anthropogenic activities along their borders and despite heavy protection (8–11). A major question is how these edge areas can be managed most effectively to best preserve both biodiversity and human livelihoods (12). Previous studies suggest that both the rate of land use change and the growth of human populations can be fastest near protected area boundaries (13–16), which accelerate the rate of edge degradation through increased livestock production, crop cultivation, and extraction of natural resources such as charcoal and bushmeat. In regions with high human density, the sharp contrast in natural resources across PA boundaries leads to “hard edges” which exacerbates human-wildlife conflicts (17), leading to two opposing intervention strategies. Fencing PAs as a form of “land sparing” from intensively used surrounding areas can solve some human-wildlife conflicts but also prevents beneficial temporary use of areas outside the reserve by wildlife, and requires intensive management that can be too costly for large reserves in developing countries (18–20). An alternative strategy involves “land sharing”, which promotes the coexistence of humans and wildlife, especially in buffer zones (21). The majority of the earth’s PAs are not fenced, questioning if anthropogenic activities at the edges are increasingly compromising the ecological processes in the core. The objective of our research is to assess if edge effects are currently undermining the ecological integrity that PAs aim to protect.

### **The concept of spatial compression in PAs (Fig.1)**

At low human population density, people can extract sufficient resources and receive additional benefits from PAs without compromising them and conversely PAs can profit from the presence of people. Under these conditions, livestock and wildlife can coexist outside core protected areas (CPAs; 22, 23). Unprotected areas (UPAs) can support ecotourism and harvesting of wildlife, while livestock keeping can create local nutrient hotspots that increase biodiversity (24, 25). This can lead to mutually beneficial relationships between people and wildlife (26) over long periods of time (27). However, steep increases in human populations (through population growth and/or migration towards CPAs) can result in unsustainable use and thus reduce wildlife populations both outside and along the edges of the CPAs (28–30). This may impose a form of habitat compression that increases wildlife densities within the CPAs by making their effective size smaller than their geographic size. Such habitat compression may result in apparently positive effects (e.g. increased wildlife densities) becoming negative in the long-term if they cause undesirable changes in the functioning and stability of the ecosystem.

Here, we show how spatial compression alters the key ecological functioning of the Serengeti-Mara ecosystem in Tanzania and Kenya, one of the largest, most iconic PAs in the world. This ecosystem is famous for its soft-edge land-sharing conservation strategies that buffer the CPAs formed by the Serengeti National Park (SNP), the Mara Reserve and several adjacent areas with similar and complementary management to the national parks (CPA: IUCN-cat. II, see (31), Table S1). The ecosystem is managed to protect the diversity of wildlife and ecological processes, foremost the migration of over 2 million large herbivores, primarily wildebeest

(*Connochaetes taurinus*), zebras (*Equus quagga*) and Thomson's gazelles (*Eudorcas thomsonii*) (32). The spatial layout of a set of protected areas with different management supports this migration (Fig. S1) by allowing animals free access to spatio-temporally variable forage within the CPA, adjacent PAs with Sustainable Resource Use (PASRU: IUCN-cat. V and VI) and UPAs. Using a combination of long-term field experiments, census data and remote sensing, we show that increasing human populations, and their accompanying livestock and land conversion practices, have "squeezed" the (migratory) grazing animals into an increasingly smaller part of the CPA. We provide evidence that compression of wildlife has resulted in increased grazing intensity in the CPA that decreases rangeland productivity, changes fire regimes, reduces soil carbon storage and alters seasonal water retention. Our study demonstrates how land use at the borders of a large PA modifies wildlife-vegetation interactions within and consequently changes multiple ecosystem processes and services in the CPA.

### **Increased human dominance outside the CPA**

From 1999 to 2012, the human population in the areas surrounding Serengeti-Mara increased by 2.4% per year on average (Fig. S2-S6; (31)). The human population growth rate was higher in the UPA along the western boundaries, inhabited by Sukuma and Kuria agro-pastoralists, compared with the PASRU along the eastern boundaries of the CPA where Maasai pastoralists herd their livestock. Concomitantly, crop agriculture expanded from 37.0% of the region in 1984 to 54.0% in 2018 (Fig. S7; Table S2-S3; (31)). The growth of the cattle population (0.9% on average per year, 2002-2012) was especially high in the wetter Tanzanian Mara Region, towards Lake Victoria (4.2% per year), despite there being very little land outside the CPA left for grazing in this area. Sheep and goat populations increased steeply in all the regions bordering the CPA (3.8% per year; Fig. S8; (31)). Concurrently, grazing lands exhibited intensifying impacts as evidenced by decreasing herbaceous vegetation green up, most notably in the PASRU, (Fig. S9-S11; (31)) and virtually no fires outside the CPA since 2005 (Fig. 2, S12-S14; (31)).

### **Expanding edge effects induce spatial compression**

We use unique and detailed data from the Narok subarea of the ecosystem to show how livestock densities increased not only close to the border but also within the CPA over the past four decades, likely displacing wild herbivores into the SNP and leading to declining densities in MMNR (Fig. 3, S15-S19, Tables S4-S6; (31)). Here, human settlement and population densities have increased enormously, especially close to the CPA boundary (note that increased people densities inside the MMNR in Fig. 3 represent park and lodge staff, not movement of local people living outside the reserve). The wildlife biomass inside the first 15km of the CPA reduced by 75% in the wet season and by 50% in the dry season from the 1970s to 2000s. The latter declines are largely due to changes in the abundance of the Loita sub-population of migratory wildebeest and zebra that traditionally use the MMNR as their dry season range. Although such detailed data are not available for the rest of the ecosystem, several indicators show that this spatial compression phenomenon happened throughout the ecosystem.

In recent years, Maasai pastoralists in the PASRU have moved their bomas towards the borders of the CPA (Fig. S20-S25; (31)) and even established bomas up to 10 km inside the CPA (Fig. 2). In addition, Maasi pastoralists with bomas outside the CPA might bring their herds on illegal multi-day grazing trips into the CPA, as opposed to short, nightly grazing trips by the agro-pastoralists on the west. The trend to push more livestock further into the CPA is probably in

response to declines in palatable forage in the remaining communal village grazing lands (30, 33).

The resulting cross-boundary human pressures also affect the extent of the migratory movements of large herbivores, a defining ecological process of the Serengeti-Mara ecosystem. Ecosystem-wide movement data obtained by GPS collaring of migratory wildebeest show avoidance of the CPA margins in the last two decades and use has especially decreased along the borders of PASRU **and concentrated at the core** (Fig. 4A-B, S26; (31)). Three lines of evidence suggest that these patterns are best explained by increased competition between migratory wildebeest and livestock.

First, the analysis of boundaries with UPAs where patrolling is medium (Fig. S1; (31)), such as the border of Maswa Game Reserve, indicates that agro-pastoralists enter the park with their livestock on a daily basis, producing an extensive network of livestock paths (Fig. 2, S22-S23, S27; (31)). This coincides with a strong reduction in maximum vegetation greenness (maxNDVI) within the first 7 km inside the CPA (>10%; Fig. 4G-H), as well as a significant decline in the area of the CPA burned in the past 16 years from 52% to 29% corresponding to 3184 km<sup>2</sup> in total (GLM:  $F_{1,14} = -5.9$ ,  $p < 0.05$ ; Fig. 4E-F). The most severe changes in maxNDVI and fire coincide with a high density of livestock paths and (temporary) livestock corrals (bomas), suggesting illegal livestock incursions into the protected area removes vegetation biomass (Fig. 2, S10, S13; (31)).

Second, these effects are ameliorated in areas with increased border control where illegal grazing is more effectively excluded. The boundaries of the UPAs with strong border control, such as the edges of the Grumeti Game Reserve, show less drastic changes in NDVI (Fig. 4, compare UPA Strong with UPA Medium), suggesting these areas are less intensively grazed by livestock. Along UPA Strong boundaries, wildebeest increased their use close to the border, whereas in the UPA Medium areas wildebeest use increased beginning at 7 km inside the border, corresponding to the distance of livestock incursions.

The third line of evidence suggesting livestock compete with wildlife comes from observing the response of wildebeest in the different PASRU boundaries (Fig. 4C-D, S26; (31)). In Narok where the intensity of use by wildebeest utilization was previously highest, wildebeest utilization has declined up to 15 km inside the CPA, while along the border with Loliondo Game Controlled Area (LGCA) the decreased use only stretches a few kilometers inside. Most notably, utilization in the Ngorongoro Conservation Area (NCA) increased in recent years. There are multiple explanations for these contrasting effects between the different PASRU. First, NCA has lower human and livestock population densities than in LGCA and Narok (Figs. S4-5, S8; (31)).

Second, the most severe food competition between livestock and wildebeest should take place during the dry season when the wildebeest reside in the Mara (34). Third, wet season competition in NCA is further reduced due to the risk of transmission of malignant catarrhal fever by calving wildebeest and the resultant avoidance of wildebeest calving sites by Maasai pastoralists. Altogether, competition between wildebeest and livestock is highest in Narok and lowest in NCA (35), suggesting the NCA boundary still functions as a soft boundary in contrast to Narok. The observed squeeze thus occurs most strongly in the dry season, a pattern that is supported by detailed surveys from Narok (Fig. 2). Wildebeest collar data show a (1) displacement of wildlife away from the dry season range in Narok and towards Northern Serengeti and the Western Corridor (Fig. S26; (31)), and (2) increasing wildebeest utilization in the UPA Strong and UPA Medium (except for the first 7 km)(Fig. 4A-B).

### **Consequences for the ecological functioning of the CPA**

In addition to the severe effects of human disturbance in the border regions of CPA, our data suggest that these compression effects (Figs. 2-4) spatially cascade to modify ecosystem processes over the entire CPA, not just the boundary. Grazing intensity (by wildlife) measured at eight long-term grazing exclosure (LTGE) sites, each with three pairs of ungrazed (exclosures) and control (unfenced) plots, across SNP (48 plots in total; Fig. S12; (31)) has increased by 16% between 2001-2016 (ca. 1.1% per year (Fig. 5A, S28A; (31))). A Generalized Linear Model with plot-pairs as subjects (blocks) and year and September-June rainfall as covariates, shows that this change is not explained by rainfall (Table S7; (31)). Concurrently, the total area burned in the CPA decreased from 55% to 34% without changes in fire management, while maxNDVI decreased by 8% on average from 0.78 to 0.71 (Fig. 5B-C). Wildebeest formerly spent the longest time on the Serengeti Plains, the Central Serengeti and parts of the Western Corridor before moving to the Mara Triangle and returning through the area bordering the LGCA. In recent years, the wildebeest distribution has extended farther south and west of the CPA into areas that receive greater rainfall and feature high wet season biomass of plants living on poorer quality soils (Fig. S26E, S28B). Increased use of such areas inside the CPA would be expected when herbivores are displaced from preferred grazing sites in Narok and LGCA as they are the only other areas with permanent water. These changes in wildebeest use, grazing intensities, area burned and maxNDVI in the core ecosystem cannot be explained by changes in wildebeest population numbers (Fig. S29; Table S8 (31)) or decreasing rainfall ((36); Fig. S30-S31; if anything, there was a trend of increasing rainfall). Changes occurred simultaneously with the increased human dominance outside the CPA and its boundary areas, and together provide strong evidence that ecological function is changing at the core of an ecosystem due to compression of wildlife.

It is unclear why this habitat compression has not resulted in an observable decline in wildebeest numbers, since the overall abundance of wildebeest is thought to be regulated by dry season food availability (34). It is possible that the trend of increasing rainfall (Figs. S30-S31; (31)) has resulted in sufficient primary productivity to still support the current densities of wildebeest (Fig. 5A). Alternatively, the wildebeest population may not be near carrying capacity, or may not yet have reached a new equilibrium (37). While the long-term population trend is relatively stable and indicative of food limitation (Fig. S29), a large percentage of the population (up to 12% year<sup>-1</sup>) is removed each year for bushmeat (38), and this offtake may dampen the role of food competition in wildebeest mortality, and potentially compensate other demographic components such as birth rates or juvenile survival. Overall, the future impacts of these changes in space use on animal numbers are uncertain and of potential concern.

The park-wide increased grazing intensities are associated with a number of ecosystem function changes. Data from the LTGE sites shows that plant biomass in grazed areas in the CPA depended much less on annual rainfall in the period 2009-2016 than over the same range of rainfall variation during the period 2001-2006 (GLM Year x Rainfall Interaction,  $X^2=5.31$ ,  $P<0.03$ ; Fig. 5A, Table S9) after accounting for the effect of grazing on biomass. Reduced vegetation responsiveness suggests that increased grazing intensities inside the park may reduce the resilience of plant productivity. Measurements of multi-year dynamics of soil organic carbon (SOC, 0-30 cm depth) in grazed plots reveal a significant unimodal response to grazing intensity (Fig. 5B), with negative changes at higher grazing intensities ( $GI>0.55$ ). This response suggests that the increased grazing intensities due to a “squeeze” effect decreases soil carbon

sequestration in Serengeti grasslands (39), which we see as a significant decline in the number of plots that sequestered more than 1 Mg C/ha between 2009-2017 (6 of 21 plots, 28.3%) than between 2001-2008 (14 of 24 plots, 58.6%) ( $X^2=4.01$ ,  $P=0.04$ ).

Other data from the LTGE experiment suggest three different ecosystem responses that might explain why compression and increased grazing intensity would yield lower resilience and carbon storage. First, higher grazing intensities were significantly associated with higher percent cover of largely unpalatable forbs and lower cover of known N-fixing species, including legumes, in grazed plots (Fig. 5C)(40). Second, as indicated by a significant quadratic regression model, higher grazing intensities shifted effects of grazers on root biomass significantly ( $P < 0.01$ ) from positive to negative (Fig. 5D). Third, effects of grazers on production of hyphae by arbuscular mycorrhizal fungi, important plant symbionts for phosphorus uptake, shifted from positive to negative as grazing intensity increased ( $P < 0.01$ ; Fig. 5E)(41). These relationships suggest that the higher grazing intensities associated with habitat compression may weaken mutualistic relationships that assist nutrient acquisition (Fig. 5C,E) and increase belowground carbon inputs (Fig. 5D,E). Furthermore, increases in unpalatable forbs are associated with lower representation of dominant grass species, possibly further exacerbating the degradation of primary productivity that supports the diverse and dominant food webs of the Greater Serengeti-Mara Ecosystem (42). These changes may signal future degradation in CPA that has already happened in human-dominated community areas.

### **The way ahead**

Today, wildlife competes with cattle for grass, generating a conflict in both UPAs where aspirations to increase cattle grazing are restricted by competition with wildlife and in PAs when cattle are moved into the park to compensate. While people were evicted from current CPAs in the 20th century, wildlife is still allowed to roam the village lands, creating potential conflict over this asymmetric historical relation. Our results illustrate that these conflicts at the periphery of large PAs can have strong impacts on the ecological functioning at the core. These results highlight the challenge in managing ecosystem edges for effective whole-ecosystem biodiversity conservation, given the current rate of human population expansion and land-use change in its surroundings.

As the GSME is among the largest PAs in Africa, the situation is likely to be considerably worse for smaller areas. The GSME is one of the few, and perhaps most iconic ecosystems whose PA boundaries were established based on ecological considerations of a larger landscape, intended to encompass migratory animals (43). However, most other PAs across Africa represent now only fragments of formerly much larger ecosystems (44). This landscape fragmentation has caused the strong decline or extinction of most large-scale migrations worldwide (45). This calls for novel strategies for improving the ecological integrity of fragmented ecosystems as well as for preserving the last remaining places where these large-scale migrations still persist.

This will require re-thinking how to maintain the integrity of ecosystem edges, especially under the rapidly increasing human densities and footprints in developing countries. For relatively intact and contiguous ecosystems such as the GSME, sustainable long-term solutions are likely to be found in ambitious land-use plans that actively manage resources beyond PA boundaries. Strategies where humans and wildlife share landscapes under conditions established and enforced by mutual agreement of local people and regional or national governments are likely the way forward. People with rural livelihoods can strongly profit from nature, and nature can profit from them. But only if neighboring communities are strongly involved in conservation

(46), preferably in long-term and locally-led programs with direct and long-term community benefits from conservation actions (47) and conservation management has long-term stability. This will require i) continued monitoring of both the ecological integrity and societal trends in the surroundings of PA's, ii) the building of more (justified) trust with local communities that they will keep sharing in the benefits of natural resource conservation, and iii) ensuring that livestock numbers, settlement and cropland expansion in the direct vicinity of core protected areas do not go beyond a point where they impair the key structure and functioning of the underlying socio-ecological system.

## References and Notes:

1. B. Worm *et al.*, Impacts of biodiversity loss on ocean ecosystem services. *Science* (80-. ). **314**, 787–790 (2006).
2. G. M. Mace, K. Norris, A. H. Fitter, Biodiversity and ecosystem services: A multilayered relationship. *Trends Ecol. Evol.* **27** (2012), pp. 19–25.
3. M. Loreau *et al.*, Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*. **294**, 804–808 (2001).
4. D. Tilman, D. Wedin, J. Knops, Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*. **379**, 718–720 (1996).
5. J. E. M. Watson, N. Dudley, D. B. Segan, M. Hockings, The performance and potential of protected areas. *Nature*. **515**, 67–73 (2014).
6. T. O. McShane *et al.*, Hard choices: Making trade-offs between biodiversity conservation and human well-being. *Biol. Conserv.* (2011), doi:10.1016/j.biocon.2010.04.038.
7. K. R. Jones *et al.*, One-third of global protected land is under intense human pressure. *Science*. **360**, 788–791 (2018).
8. T. H. Ricketts *et al.*, Pinpointing and preventing imminent extinctions. *Proc. Natl. Acad. Sci.* **102**, 18497–18501 (2005).
9. C. A. Runge *et al.*, Protected areas and global conservation of migratory birds. *Science* (80-. ). **350**, 1255–1258 (2015).
10. C. N. Jenkins, K. S. Van Houtan, S. L. Pimm, J. O. Sexton, US protected lands mismatch biodiversity priorities. *Proc. Natl. Acad. Sci.* **112**, 5081–5086 (2015).
11. I. D. Craigie *et al.*, Large mammal population declines in Africa's protected areas. *Biol. Conserv.* **143**, 2221–2228 (2010).
12. R. DeFries, A. Hansen, B. L. Turner, R. Reid, J. Liu, Land use change around protected areas: Management to balance human needs and ecological function. *Ecol. Appl.* **17** (2007), pp. 1031–1038.
13. G. Wittemyer, P. Elsen, W. T. Bean, A. C. O. Burton, J. S. Brashares, Accelerated human population growth at protected area edges. *Science* (80-. ). **321**, 123–126 (2008).
14. L. Naughton-Treves, J. Alix-Garcia, C. A. Chapman, Lessons about parks and poverty from a decade of forest loss and economic growth around Kibale National Park, Uganda. *Proc. Natl. Acad. Sci.* **108**, 13919–13924 (2011).
15. A. B. Estes, T. Kuemmerle, H. Kushnir, V. C. Radeloff, H. H. Shugart, Land-cover change and human population trends in the greater Serengeti ecosystem from 1984–2003. *Biol. Conserv.* **147**, 255–263 (2012).
16. K. S. Andam, P. J. Ferraro, K. R. E. Sims, A. Healy, M. B. Holland, Protected areas reduced poverty in Costa Rica and Thailand. *Proc. Natl. Acad. Sci.* **107**, 9996–10001 (2010).
17. R. Woodroffe, S. Thirgood, A. Rabinowitz, The impact of human – wildlife conflict on natural systems. *People Wildlife, Confl. or Co-existence?*, 1–12 (2005).
18. M. J. Somers, M. W. Hayward, *Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes?* (2012).
19. C. Packer *et al.*, Conserving large carnivores: Dollars and fence. *Ecol. Lett.* **16**, 635–641 (2013).
20. J. O. Ogutu, N. Owen-Smith, H. P. Piepho, B. Kuloba, J. Edebe, Dynamics of ungulates in relation to climatic and land use changes in an insularized African savanna ecosystem. *Biodivers. Conserv.* **21**, 1033–1053 (2012).
21. B. Phalan, M. Onial, A. Balmford, R. E. Green, Reconciling food production and biodiversity conservation:



- Land sharing and land sparing compared. *Science* (80-. ). **333**, 1289–1291 (2011).
22. M. Y. Said *et al.*, Effects of extreme land fragmentation on wildlife and livestock population abundance and distribution. *J. Nat. Conserv.* **34**, 151–164 (2016).
  23. J. O. Ogutu, Changing Wildlife Populations in Nairobi National Park and Adjoining Athi-Kaputiei Plains: Collapse of the Migratory Wildebeest. *Open Conserv. Biol. J.* **7**, 11–26 (2013).
  24. C. Riginos *et al.*, Lessons on the relationship between livestock husbandry and biodiversity from the Kenya Long-term Exclosure Experiment (KLEE). *Pastoralism.* **2** (2012), , doi:10.1186/2041-7136-2-10.
  25. V. Vuorio, A. Muchiru, R. S. Reid, J. O. Ogutu, How pastoralism changes savanna vegetation impact of old pastoral settlements on plant diversity and abundance in south western Kenya. *Biodivers. Conserv.* **23** (2014), doi:10.1007/s10531-014-0777-4.
  26. K. Homewood, W. A. Rodgers, Maasailand Ecology. Pastoral development and wildlife conservation in Ngorongoro, Tanzania. *Cambridge Stud. Appl. Ecol. Resour. Manag.* (1991), doi:Doi 10.1007/Bf01059514.
  27. H. Olf, J. G. C. Hopcraft, in *Serengeti III. Human impacts on ecosystem dynamics.*, A. R. E. Sinclair, C. Packer, S. A. R. Mduma, J. Fryxell, Eds. (University of Chicago Press, Chicago, 2008).
  28. S. L. Lewis, D. P. Edwards, D. Galbraith, Increasing human dominance of tropical forests. *Science* (80-. ). **349** (2015), pp. 827–832.
  29. J. S. Brashares, P. Arcese, M. K. Sam, Human demography and reserve size predict wildlife extinction in West Africa. *Proc. R. Soc. B Biol. Sci.* **268**, 2473–2478 (2001).
  30. J. O. Ogutu, H. P. Piepho, H. T. Dublin, N. Bhola, R. S. Reid, Dynamics of Mara-Serengeti ungulates in relation to land use changes. *J. Zool.* **278**, 1–14 (2009).
  31. M. Materials, Materials and methods are available as supplementary materials at the Science website.
  32. A. R. E. Sinclair *et al.*, Long-term ecosystem dynamics in the Serengeti: Lessons for conservation. *Conserv. Biol.* **21**, 580–590 (2007).
  33. B. Butt, A. Shortridge, A. M. G. A. WinklerPrins, Pastoral herd management, drought coping strategies, and cattle mobility in Southern Kenya. *Ann. Assoc. Am. Geogr.* **99**, 309–334 (2009).
  34. S. A. R. Mduma, A. R. E. Sinclair, R. Hilborn, Food regulates the Serengeti wildebeest: A 40-year record. *J. Anim. Ecol.* **68**, 1101–1122 (1999).
  35. W. O. Odadi, M. K. Karachi, S. A. Abdulrazak, T. P. Young, African wild ungulates compete with or facilitate cattle depending on season. *Science* (80-. ). (2011), doi:10.1126/science.1208468.
  36. G. S. Bartzke *et al.*, Rainfall trends and variation in the Masai Mara ecosystem and their implications for animal population and biodiversity dynamics. *PLoS One.* **in press** (2018).
  37. J. M. Diamond, Biogeographic Kinetics: Estimation of Relaxation Times for Avifaunas of Southwest Pacific Islands. *Proc. Natl. Acad. Sci.* (1972), doi:10.1007/s10029-013-1119-2.
  38. D. Rentsch, C. Packer, The effect of bushmeat consumption on migratory wildlife in the Serengeti ecosystem, Tanzania. *Oryx.* **49**, 287–294 (2015).
  39. R. M. Holdo *et al.*, A Disease-Mediated Trophic Cascade in the Serengeti and its Implications for Ecosystem C. *PLoS Biol.* **7**, e1000210 (2009).
  40. M. E. Ritchie, R. Raina, Effects of herbivores on nitrogen fixation by grass endophytes, legume symbionts and free-living soil surface bacteria in the Serengeti. *Pedobiologia (Jena).* **59**, 233–241 (2016).
  41. J. R. Propster, N. C. Johnson, Uncoupling the effects of phosphorus and precipitation on arbuscular mycorrhizas in the Serengeti. *Plant Soil.* **388**, 21–34 (2015).
  42. S. N. De Visser, B. P. Freymann, H. Olf, The Serengeti food web: Empirical quantification and analysis of topological changes under increasing human impact. *J. Anim. Ecol.* **80**, 484–494 (2011).
  43. S. Thirgood *et al.*, Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Anim. Conserv.* **7**, 113–120 (2004).
  44. R. DeFries, K. K. Karanth, S. Pareeth, Interactions between protected areas and their surroundings in human-dominated tropical landscapes. *Biol. Conserv.* **143**, 2870–2880 (2010).
  45. G. Harris, S. J. Thirgood, J. G. C. Hopcraft, J. P. G. M. Cromsigt, J. Berger, Global decline in aggregated migrations of large terrestrial mammals. *Open Acces.* **7**, 55–76 (2009).
  46. I. Palomo *et al.*, Incorporating the social-ecological approach in protected areas in the anthropocene. *Bioscience.* **64**, 181–191 (2014).
  47. R. M. Pringle, Upgrading protected areas to conserve wild biodiversity. *Nature.* **546** (2017), pp. 91–99.
  48. A. R. E. Sinclair, *Serengeti: dynamics of an ecosystem* (University of Chicago Press, 1979).
  49. F. Darling, An Ecological Reconnaissance of the Mara Plains in Kenya Colony. *Wildl. Monogr.* **5** (1960).
  50. N. Simon, *Between the sunlight and the Thunder: The Wild Life of Kenya* (Collins, London, 1962).
  51. WPU, “Masai Mara National Reserve Management Plan” (Nairobi, Kenya, 1983).

52. M. Walpole, G. Karanja, N. W. Sitati, N. Leader-Williams, Wildlife and people: Conflict and conservation in Masai Mara, Kenya. *IIED Wildl. Dev. Ser.* (2003).
53. F. F. Mol, *Maasai Mara* (Privately published, Nairobi, Kenya, 1980).
54. ILRI, ILRI GIS Services (2011), (available at <http://192.156.137.110/gis/>).
55. KNBS, “Kenyan Population Census, Household and Density 2009” (Nairobi, Kenya, 2009).
56. TNBS, “Population and Housing Census: Population Distribution by Administrative Areas” (Dar Es Salaam, Tanzania, 2013).
57. A. Janz, S. van der Linden, B. Waske, P. Hostert, in *5th EARSeL Workshop on Imaging Spectroscopy* (2007), p. 5.
58. T. Kuemmerle *et al.*, European Bison habitat in the Carpathian Mountains. *Biol. Conserv.* **143**, 908–916 (2010).
59. ESRI, ArcGIS Desktop: Release 10.5 (2015).
60. TNBS, “National sample census of agriculture 2002/2003” (Dar Es Salaam, Tanzania, 2007).
61. J. O. Ogutu *et al.*, Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: What are the causes? *PLoS One.* **11** (2016), doi:10.1371/journal.pone.0163249.
62. T. M. Anderson, M. E. Ritchie, S. J. McNaughton, Rainfall and soils modify plant community response to grazing in Serengeti National Park. *Ecology.* **88**, 1191–1201 (2007).
63. K. Didan, A. H. University of Arizona, U. of T. Sydney, M. S.- NASA, MOD13Q1 - MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid. *NASA LP DAAC* (2015), p. 1.
64. L. Giglio, T. Loboda, D. P. Roy, B. Quayle, C. O. Justice, An active-fire based burned area mapping algorithm for the MODIS sensor. *Remote Sens. Environ.* **113**, 408–420 (2009).
65. E. M. Kanga, J. O. Ogutu, H. P. Piepho, H. Olff, Hippopotamus and livestock grazing: influences on riparian vegetation and facilitation of other herbivores in the Mara Region of Kenya. *Landsc. Ecol. Eng.* **9**, 47–58 (2013).
66. M. J. Coe, D. H. Cumming, J. Phillipson, Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia.* **22**, 341–354 (1976).
67. J. S. Horne, E. O. Garton, S. M. Krone, J. S. Lewis, Analyzing animal movements using Brownian bridges. *Ecology.* **88**, 2354–2363 (2007).
68. H. Sawyer, M. J. Kauffman, R. M. Nielson, J. S. Horne, Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecol. Appl.* **19**, 2016–2025 (2009).
69. J. G. C. Hopcraft *et al.*, Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecol. Monogr.* **84**, 355–372 (2014).
70. C. Funk *et al.*, The climate hazards infrared precipitation with stations - A new environmental record for monitoring extremes. *Sci. Data.* **2** (2015), doi:10.1038/sdata.2015.66.
71. T. Hengl *et al.*, Mapping soil properties of Africa at 250 m resolution: Random forests significantly improve current predictions. *PLoS One.* **10** (2015), doi:10.1371/journal.pone.0125814.
72. S. S. N. Wood, *Generalized Additive Models: An Introduction with R.* (2017; <https://books.google.com/books?id=GbzXe-L8uFgC&pgis=1>).
73. K. E. Veblen, Impacts of traditional livestock corrals on woody plant communities in an East African savanna. *Rangel. J.* **35**, 349–353 (2013).
74. Google, Google Earth Pro. (2015).
75. M. E. McSherry, thesis, Syracuse University (2015).
76. N. A. C. Cressie, *Statistics for Spatial Data (revised edition)* (Wiley, New York, 1993).
77. G. M. Jolly, Sampling Methods for Aerial Censuses of Wildlife Populations. *East African Agric. For. J.* **34**, 46–49 (1969).
78. J. G. C. Hopcraft *et al.*, in *Serengeti IV: Sustaining biodiversity in a coupled human-natural system* (2015).
79. R. H. Lamprey, R. S. Reid, Expansion of human settlement in Kenya’s Maasai Mara: What future for pastoralism and wildlife? *J. Biogeogr.* **31**, 997–1032 (2004).
80. M. Løvschal *et al.*, Fencing bodes a rapid collapse of the unique Greater Mara ecosystem. *Sci. Rep.* **7** (2017), doi:10.1038/srep41450.
81. J. G. C. Hopcraft, T. M. Anderson, S. Pérez-Vila, E. Mayemba, H. Olff, Body size and the division of niche space: Food and predation differentially shape the distribution of Serengeti grazers. *J. Anim. Ecol.* (2012), doi:10.1111/j.1365-2656.2011.01885.x.

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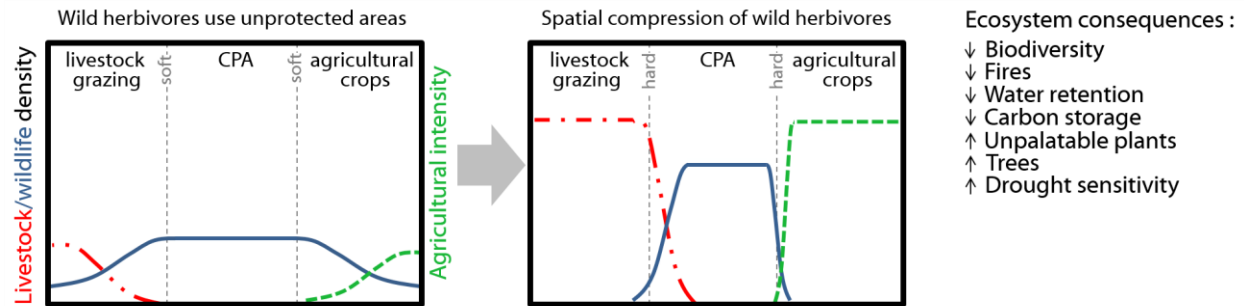
## **Supplementary Materials:**

Materials and Methods

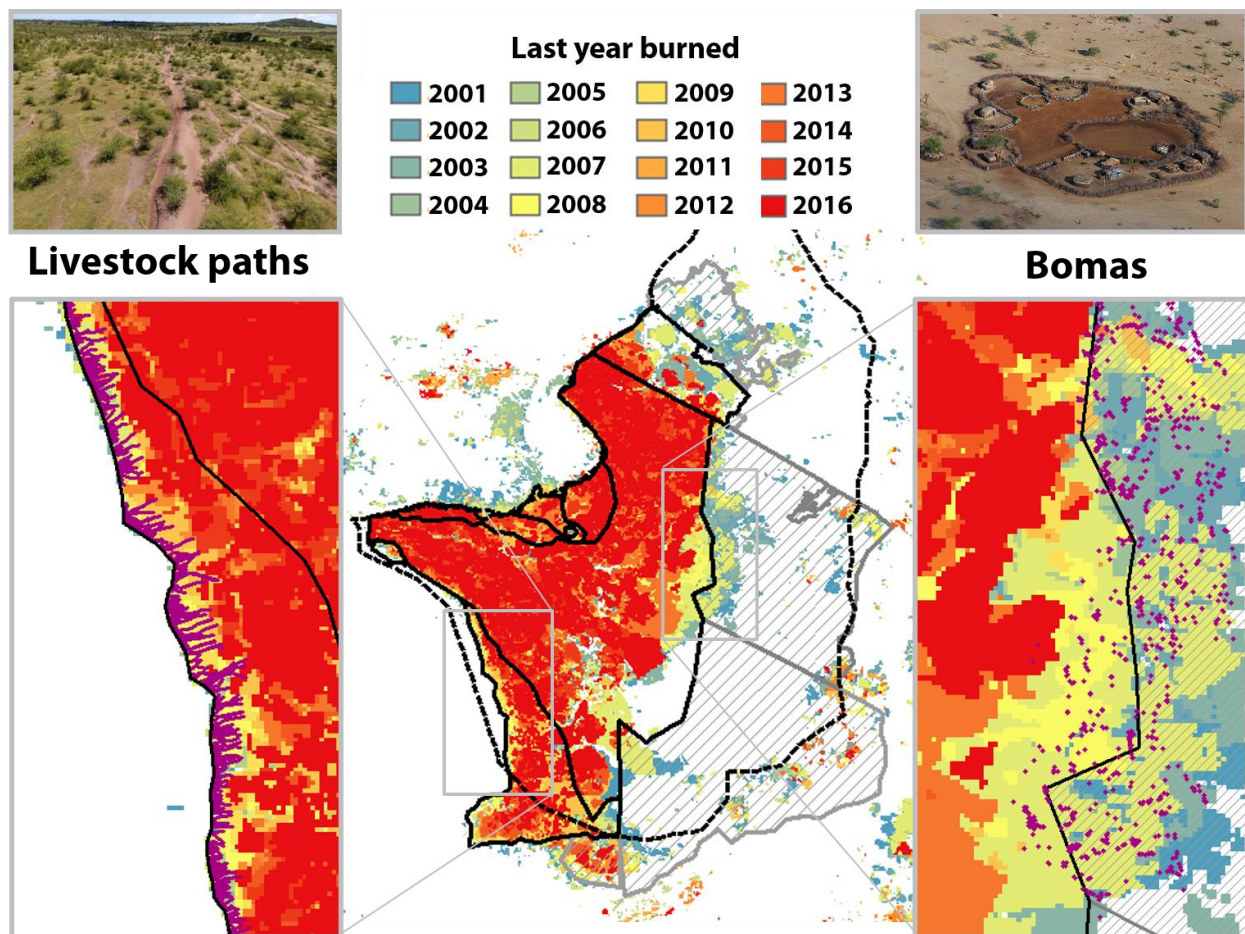
Figures S1-S31

Tables S1-S9

References (48-81)

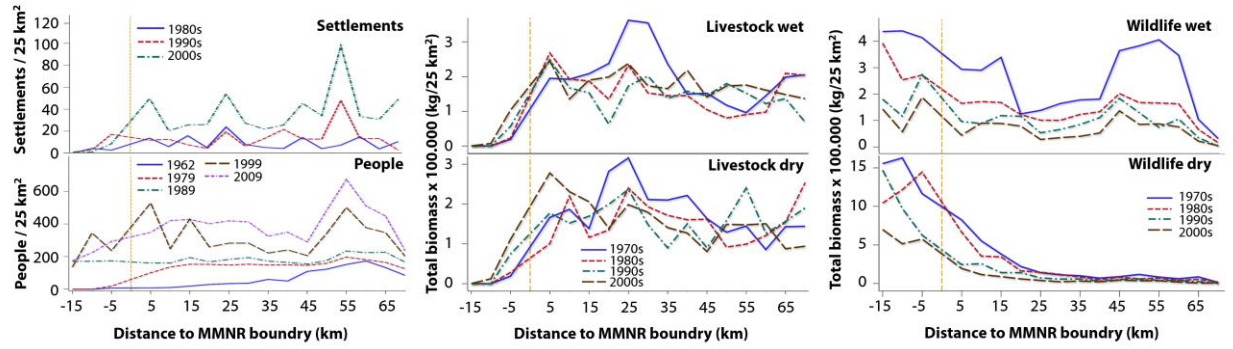


**Fig. 1. The concept of spatial compression in protected areas.** Unsustainable activities outside a soft-edge core protected area (CPA) resulting from human population growth spatially compress wildlife, leading to more intense use of protected land and multiple possible consequences for the magnitude and stability of ecosystem processes and services. Increased human population, livestock densities and/or agricultural intensities convert soft borders that effectively extend the CPA (left figure) into hard borders that effectively compress the CPA (right figure). Lines represent hypothesized wildlife (blue) and livestock (red) densities and agricultural intensity (green).



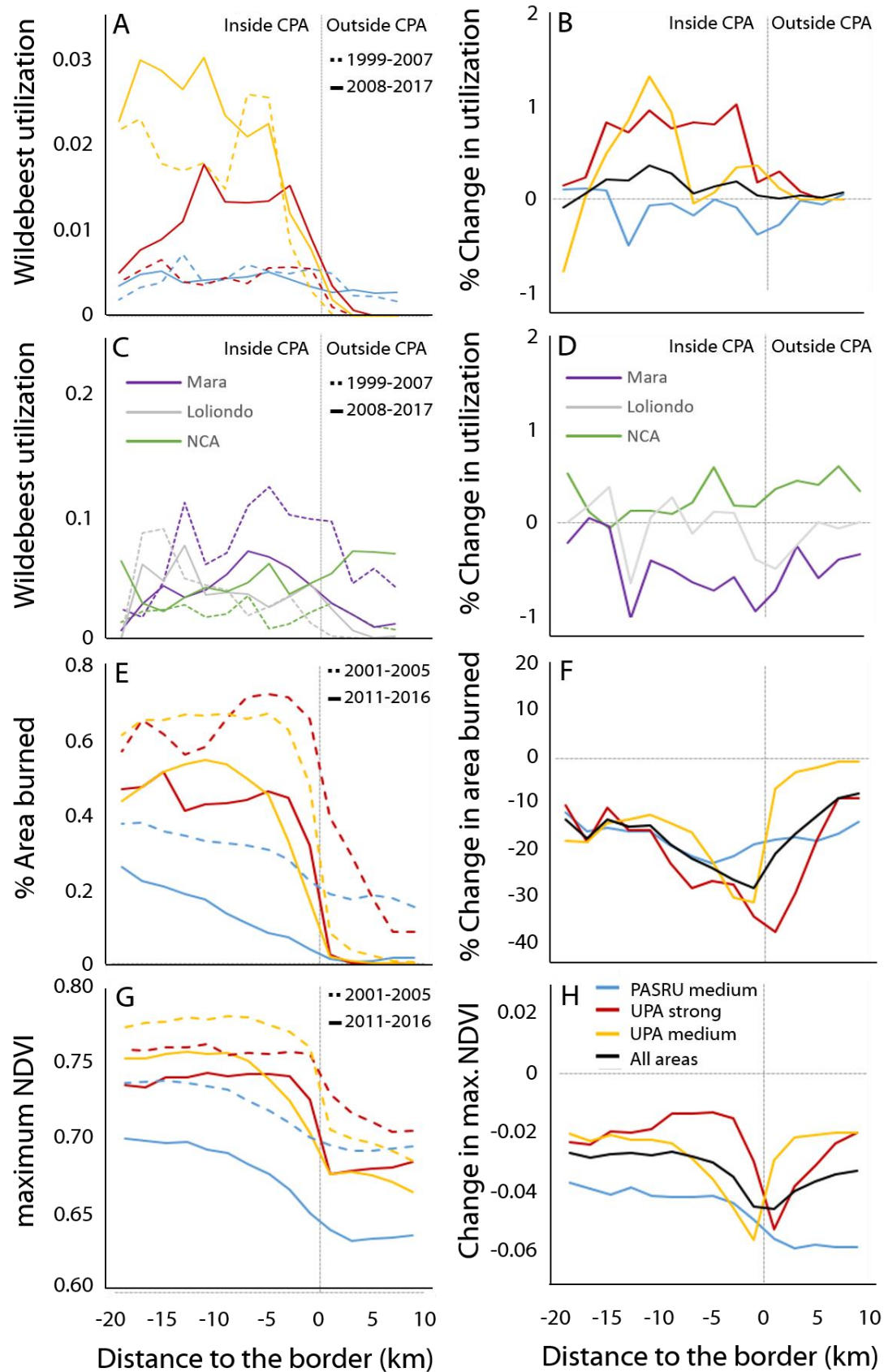
**Fig. 2. Spatial compression of burned area in the Greater Serengeti-Mara Ecosystem.**

Different colors represent the last year each pixel burned between 2001 (blue) and 2016 (red) visualized using the MODIS burned area product. Magnifications show the same map overlaid with livestock paths (left) and bomas (right). Solid black lines represent borders of Core Protected Areas (CPAs). Grey hatched areas are Protected Areas of Sustainable Resource Use (PASRU) inhabited by people and grazed by livestock. The black dashed line is the boundary of the Greater Serengeti-Mara Ecosystem that represents the area formerly used by the migratory wildlife.



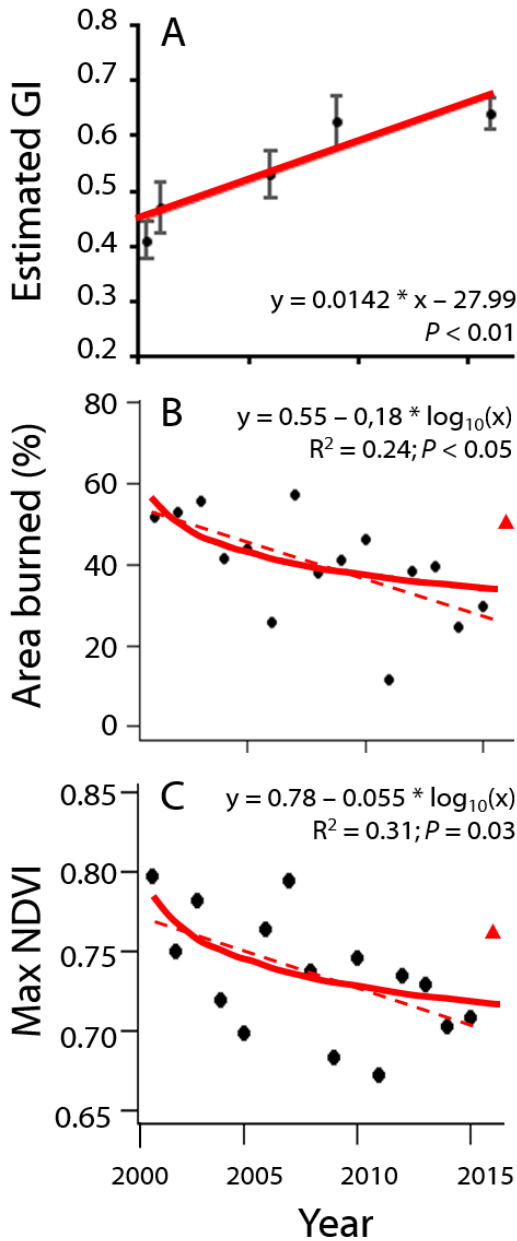
**Fig. 3. Spatial expansion of humans, livestock and the compression of wild herbivores over multiple decades.** Wildlife and livestock trends shown for both wet (top) and dry (bottom) season. Density estimates are plotted against distance to the border of Masai Mara National Reserve (MMNR) covering the first 15km inside the MMNR and 70km outside. Human settlement, people and livestock densities increase through time close to the border and even inside the MMNR. At the same time, wildlife densities decline, especially in the dry season, and these effects stretch increasingly farther into the MMNR.



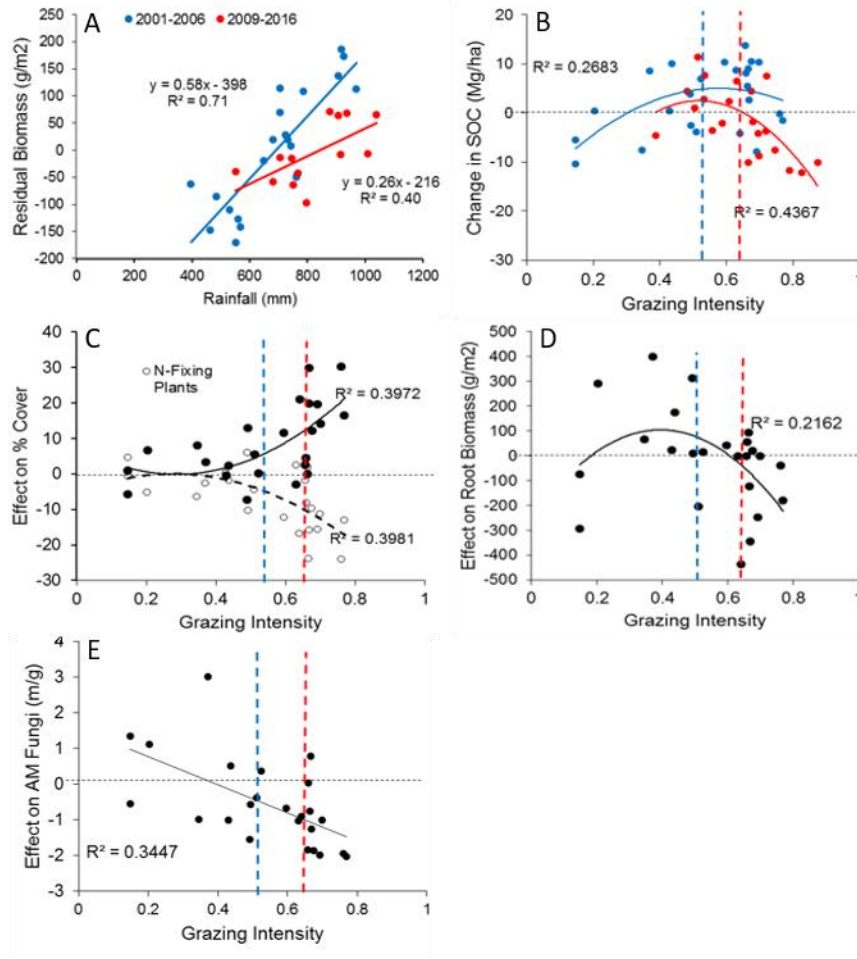


**Fig. 4. Changes in wildebeest occupancy, fire and vegetation greenness in the border regions of the Core Protected Areas (CPAs).** Wildebeest utilization between 1999-2007 and 2008-2017 (A, C), mean area burned between 2001-2005 and 2011-2016 (E), mean maxNDVI between 2001-2005 and 2011-2016 (G) and the change between the two periods (B,D,F,H) as a function of distance to the border for three different border types between CPA and: 1) Protected Area with Sustainable Resource Use (PASRU) with medium border control against illegal activities (PASRU medium, blue line), 2) unprotected areas (UPA) with strong border control (UPA strong, red line), 3) UPA with medium border control (UPA medium, orange line). Panel C and D show the same information as the PASRU (blue lines) in panel A and B but now split up for the three different PASRU areas. Black line represents the overall weighted mean. Data covers both the Tanzanian and Kenyan side of the ecosystem.





**Fig. 5. Changes in grazing intensity, burned area and maxNDVI between 2001 and 2016 for the entire area designated as Core Protected Area.** A) Grazing intensity (GI; mean  $\pm$  SE), measured through herbivore exclosures, increases by 1.08% per year on average. B) Area burned decreased by 40% in 16 years time (solid red line). C) MaxNDVI decreased by 8% in 16 years time. The burned area and maxNDVI increased in 2016 (red triangle) due to management actions in eastern Serengeti National Park. Excluding this data point results in a stronger correlation and more explained variation (dashed red lines; Area burned= $0.53-0.017*\text{years}$ ,  $R^2=0.38$ ,  $P=0.01$ ; maxNDVI= $0.77-0.047*\text{years}$ ,  $R^2=0.33$ ,  $P=0.03$ ).



**Fig. 6. Consequences of increased grazing for ecosystem processes.** Data from 2001-2017 in the Serengeti Long-Term Grazing Exclusion experiment (LTGE; 8 sites with three exclusion-control plot pairs,  $N = 24$ ). Linear models with quadratic functions contain significant coefficients ( $P < 0.01$ ), and fit significantly better than straight lines ( $R^2$  improvements  $> 0.2$ ). Vertical dashed lines represent mean grazing intensity across all sites in 2001-2008 (blue) and 2009-2016 (red). A) Residual aboveground biomass averaged across grazed plots at each site after accounting for the influence of grazing intensity in a GLM, exhibits significant ( $P < 0.01$ ) relationships with CHIRPS satellite-estimated rainfall across 8 sites in 2001, 2002, and 2006 (blue points,  $N=21$ ), at 7 sites in 2009 and 6 sites in 2016 (red points,  $N=13$ ). Slopes are significantly different ( $P < 0.04$ ). B) Changes in soil organic carbon (SOC) in each grazed plot from 2001 to 2008 (blue circles,  $N=24$ ) and 2009 to 2017 (red circles,  $N=21$ ). C-E) Effects of excluding herbivores in plot pairs (control–exclusion measure) at different mean grazing intensities (measured in 2006 and 2009) on C) percent cover of N-fixing plants, both grasses and legumes (open circles) and low palatability forb species (solid circles), D) root biomass and E) production of hyphae of arbuscular mycorrhizal (AM) fungi.



## Supplementary Materials for

### **The Serengeti squeeze: cross-boundary human impacts compromise an iconic protected ecosystem**

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